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A CONTRIBUTION TO THE KNOWLEDGE OF THE BIONOMICS OF BREMUS IMPATIENS (CRESSON). (HYMENOPTERA.)

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A. INTRODUCTION.

The present paper is the second of a series of papers dealing with the biology of the North American species of bumblebees. In the first paper (1928), the salient features of the bionomics of *Bremus bimaculatus* (Cresson) were recorded, detailed tables presented to show the development of the various castes from eggs to adults, and statements given regarding technique used in securing data for tables and other information. For the sake of brevity no tables are included in this paper and no introductory matter is repeated. The information herein presented is based upon experiments and observations made chiefly in 1919 and 1920, coupled with subsequent observations and a survey of the literature of our subject up to the present time.

During the course of my investigations of the biology of bumblebees, I have never had the opportunity to study in detail a nest of this species established under natural conditions. In 1919, there was a fair prospect that such an opportunity would come when a queen of this species occupied one of my domiciles buried near White Heath, Illinois. On May 17, this domicile contained the mother queen and a cluster of cocoons, but two weeks later when the nest was removed a field mouse was in possession of the domicile and the comb had been completely destroyed. In the laboratory, however, five nests of this species have been under close observation. Since the main features of the biological histories of bumblebees have been found to be the same regardless of

whether the nests are started in artificial nests in the laboratory or out-of-doors under natural conditions, the data obtained by their study give a normal biological appraisement of this species. One of these nests, or colonies (Experiment 6, 1919), was studied in considerable detail, and data concerning the development from eggs to adults of workers and males obtained almost daily by methods reported in a recent article (1928). Before passing to a study of condensed tabulations necessary for an understanding of conclusions regarding the developmental stadia, a brief description should be presented of the start and growth of the colonies under observation; particularly the colony studied in much detail (Experiment 6, 1919).

B. Specific Life History Studies.

1. Experiment 6, 1919.

On April 18, 1919, a queen of *B. impatiens* was captured in the Brownfield Woods near Urbana, Illinois, and brought back alive to the laboratory in a small paper collapsible box. She was immediately placed in a small glass aquarium jar, screened on top, containing a supply of food. This preliminary procedure was intended to make the queen become "broody," a method previously explained in the Biological Bulletin (Frison, 1927a). Four days later she was removed to a rearing box containing an artificial nest, a wax honey pot, and a lump of pollen. These artificial nests are used to induce queens to start colonies under controlled conditions, and have already been described in detail in the Biological Bulletin (Frison, 1927a). The next day after being placed in the artificial nest the queen began to manifest an intense interest in the nest. On this date, April 23, she began the construction on the pollen lump of egg cells similar to those described for *B. bimaculatus* (Frison, 1928), and slightly altered the artificial honey pot. On the following day these cells were capped over and upon examination were found to contain creamy-white eggs. According to my notes, these first eggs were all laid in separate wax-pollen cells, about three millimeters long, two to three millimeters wide and two millimeters deep. The pollen for their construction came from the lump on which the cells were formed. The wax, however, had a different origin, for it was produced by the queen and scraped from her body onto the pollen lump. On April 26, the cells still contained eggs, but when next opened, on

May 1, they contained larvae. These egg cells were not opened during the interim between April 26 and May 1 through fear of causing the queen to desert her eggs. The eggs probably hatched the 29th or 30th of April.

In spite of being disturbed intermittently for about two hours on May 2, when motion pictures were taken under high power lights of the comb and queen, her majesty continued to show an interest in her brood. The stage of development of the comb at this time is well shown in figure 1. By the 10th of May, the larvae had progressed so far as to spin cocoons and the queen had laid more eggs in new egg cells built on top of the cocoons. Each of these egg cells contained from two to four eggs, laid almost horizontally side by side and contiguous to one another in the cell. Evidently her early habit of laying one egg in a cell, so reminiscent of the solitary bees, had ceased. At this period in the development of the colony, a broad shallow groove was in evidence on the top of the comb. This groove owed its origin to a peculiar habit of the queen which always assumed the same position on her incipient comb when incubating her first brood. The taking of motion pictures of this queen on the nest and of still pictures with the queen removed on May 9 and 10, luckily, once again did not cause the queen to forsake her brood. Figure 2 shows the comb as it appeared on May 10, before the wax and pollen was removed from the first cocoons. This figure shows, also, the eggs in the egg cells, and the groove or "saddle" occupied by the queen when brooding on her first larval cells. On May 12, the honey pot was again altered by the queen so that it was capped on top with somewhat of a recurved hood. The next day a new egg cell, much larger than those made first, was constructed, and on May 14, this cell was capped and contained two eggs. The following day the first worker emerged. The fact that this first worker was of normal size served not only as an indication that the queen was being properly fed but that the queen was also properly feeding her young. A total of five workers emerged by May 18. On this date, more eggs were laid and the presence of some fairly well-developed larvae was noted. These larvae undoubtedly came from eggs laid on May 10. Not content with the single artificial honey pot, on the 19th of May the workers made an additional one of wax and pollen adjacent to the artificial one. The 29th of May, disclosed two additional workers; the colony at this time consisting of the mother queen, seven workers, larvae and eggs.

The colony had now become so large and well established that a detailed study of the duration of the various developmental stages was begun of this last-mentioned date.

The addition of numerous wax-pollen honey pots accompanied the general and gradual increase in size of the comb. On May 25, there were six of these honey pots, three on each side of the artificial one, and all separate from the comb. A pillar of wax and pollen had also been constructed to connect the comb with the wax-lined roof of the artificial nest, and as a support served to steady the comb. At this date it was no longer necessary to remove the queen when examining the comb, because she showed no inclination to fly from the nest. Occasionally, a whiff of my breath brought forth a protest in the form of a vigorous buzzing, but she soon began brooding again over the comb with her head nestled down between the cocoons as if to avoid the light. The increase in the development of the comb since May 10 is well shown in figure 3, a photograph taken on June 10. By June 11, the colony contained twenty-two workers and was sufficiently advanced to allow the bees their freedom for the gathering of nectar and pollen. I may add that the workers were becoming very vicious and it required considerable time and patience to remove them one by one each day before examining the comb; a necessary procedure to avoid being stung.

After being allowed their liberty the workers speedily took advantage of their privilege and were soon bringing in supplies of honey and pollen. More wax-pollen pillars for supporting the comb were constructed and also honey pots of the same material on the outer edge of the comb. As soon as the full-grown larvae spun their cocoons the workers removed the wax and pollen covering them and used it to good advantage elsewhere. At this stage in the development of the colony, honey was being used in large quantities and scarcely any was to be found in the honey pots in the morning. Pollen was apparently less in demand and some of it was stored in empty cocoons. The exceedingly tall honey pots on the outer edge of the comb was a peculiarity of this nest during the middle of June. By June 16, the average number of eggs in a cell had increased to five, and the most favored place for constructing the new egg cells was on the tops of newly spun cocoons. The comb continued to grow so rapidly that on June 26 it was necessary to remove the colony to one of my large observation boxes.

The growth of the comb and the increase in number of workers did not suffer as a result of allowing the bees their freedom and the discontinuance on my part of supplying them with food, and by the 3rd of July I found myself obliged to remove more than fifty workers every time I wished to examine the comb. Several fairly hot days about this time so increased the temperature in the nest that some of the bees resorted to fanning the comb with their wings; thus creating an air movement for the ventilation of the nest. This ventilating of the nest is responsible for the myth of the "trumpeter" bee, which according to the celebrated Hoffer (1883) aroused its companions to their work. If I disturbed the nest by blowing into the entrance or jarring the box containing the nest, the large workers were the first to fly out in defense of their home. A gradual increase in the size of the workers was evident as the season advanced, and by July 9, many very large workers appeared. It is also worth recording that at this time, for the first time, a real surplus of honey existed in the nest. This was stored in specially made honey pots and in empty cocoons in the center of the comb. A surplus of pollen also existed and continued to accumulate and to be stored as before in empty cocoons. The old mother queen now was more prolific than ever and scarcely a day passed when she did not lay eggs. In fact, between July 4 and the morning of July 7, ten new egg cells were fashioned and an average of six eggs laid in each cell. This is at the rate of about twenty eggs a day. The fact that these eggs all produced workers is proof that none of them were laid by workers.

During the latter part of July, the accumulation of a surplus of honey and pollen continued unabated. The only change in the appearance of the comb, except the increase in its size, was the development of a wax-pollen sheet or thin wall on the side of the comb nearest the entrance. This was apparently built to exclude light. By the first of August, the old mother queen began to show, by the loss of hair on the dorsum of her abdomen, the effects of her brood rearing and comparative old age. At nine o'clock on the morning of August 2, one hundred and nine workers were in the nest and additional ones were foraging in the field. The presence of so many workers in the nest greatly increased the amount of preliminary work necessary before the comb could be closely examined, and the increase in number of egg, larval and pupal cells naturally lengthened the time required for the

taking of data regarding the developmental stadia. On August 11, the nest contained 116 workers in addition to an unknown number foraging in the field. At this time the colony reached its "climax" of worker production and from then on the number of workers gradually diminished. The gradual loss of hair on the dorsum of the queen, first noticed about the first of August, had proceeded so far by this time that a large portion of the dorsum of the thorax and nearly the entire dorsum of her abdomen was nude. Besides the workers and mother queen, the nest contained on this date 29 good cocoons, fifty-six larvae in various stages of development, and fourteen egg cells containing an average of three to four eggs.

The first males, twelve in number, were found in the nest on August 17. Five days later I found but eighty-eight workers in the nest, a smaller proportion than existed on August 11. There still remained a surplus of honey and pollen at this time and some pollen was being stored in the wax-pollen cells on the edge of the comb as well as in empty cocoons. On this same date, several wax-pollen cells—larger than any egg cells thus far made but smaller than any of the honey or pollen storage cells—were built on the tops of cocoons. A small quantity of loose pollen was placed in the bottom of each of these. Because of their size I was not at first certain whether these cells were for the reception of eggs or pollen. Their position clearly indicated that they were egg cells, but the pollen was something I had never seen thus placed in them by this species. Furthermore, their diameter of about seven millimeters was unusual for the egg cells of this species. The male population had by now greatly increased and on September 5 sixty-four of them were found in the nest, besides a few additional ones which retreated so deeply into the labyrinth of comb that they could not be extricated without injuring the comb. On this same day eggs were discovered in the large wax-pollen cells first noticed on August 22. The decrease in workers was now very manifest, and at this time but nineteen were found in the nest. Figure 4 is an illustration of the comb as it looked on September 6; a period of about four months and a half since the mother queen first started the nest. Comparing figure 4 with figure 3, the latter taken on June 10, the increase in the size of the comb is evident. Another view of the comb as shown in figure 4 is given in figure 5, except that the comb is shown in the artificial nest and the large observation box into which it was transferred

on June 26. On September 7, the old queen died and a short time afterwards she was dragged into a corner of the nest by her worker offspring. It was not until after the queen died that there were signs in this nest of workers developing egg-laying habits. On September 16, one of the few remaining workers seemed to show an interest in the comb and certain cells containing eggs. These eggs were certainly laid by workers, for the cells were built after the death of the old mother queen.

In keeping with the gradual decline in numbers of bees in the nest was the increase in numbers of the bumblebee wax-moth (*Vitula edmandsii* Packard), and due to the work of their larvae the once large and neat-appearing comb had rapidly deteriorated by the end of September.

2. Experiment 11, 1919.

The queen used in Experiment 11, 1919, was captured on April 16 in the Brownfield Woods, near Urbana. For several days following her capture, she was confined with several other queens in a glass aquarium jar containing a liberal food supply to make her become "broody." Then on April 22, she was placed with another queen of the same species in an artificial nest. During her brief stay in the glass jar this queen killed two other queens of her own species and soon after being placed in the artificial nest with another queen she continued her murderous career by killing the other queen. Because she did not exhibit signs of interest in this artificial nest, she was confined once again in the bell jar. On May 16 she was placed for the second time in an artificial nest, but this time without another queen to arouse her propensity for killing. On May 18, the queen exhibited a great interest in the nest and constructed an egg cell on the pollen lump. This was similar in all details to the one first made by the queen in Experiment 6, 1919. Thereafter her interest in the nest continued, and on May 19 there were three egg cells on the pollen lumps. Fear of disturbing her was responsible for neglecting a count of the number of eggs laid in these first cells. Judging from the size of the cells, the number of the eggs must have been very small. Larvae were first noticed on May 24 and from then on they grew rapidly. Eight days after the larvae were first observed two of them spun cocoons and a third did so the following day. The fact that from the first egg cells there were eventually produced

but three workers is further evidence that the first three cells contained only a few eggs, and perhaps but one each. As soon as the first two cocoons were spun on June 1, the queen constructed a new egg cell on one of them. On June 2, this egg cell was closed and contained four eggs. The same day the third larva spun its silken pupal case. Five days later, additional egg cells were present on the cocoons.

The first worker emerged on June 10, one more on June 11, and a third on June 13; all seemed normal in every respect. By the middle of June the nest contained the mother queen, three workers, larvae and eggs. At this time, when the colony was progressing so nicely, the queen accidentally lost a leg and this seemed to have a bad effect on the further development of the entire colony. Nevertheless, the queen with the help of two workers (one of them escaped on June 19 and never found its way back to the nest) continued her work as well as possible. More eggs were laid on June 26, but the colony was doomed, as the queen was scarcely able to perform her duties. Egg-laying continued, however, and the queen even laid some eggs on July 3 in a cell built of honey bee wax, separate from the comb, on the wax-lined floor of the nest. The first week of July, after transference of the comb and bees to another nest, the colony seemed to acquire a new lease on life. In one egg cell, first discovered on July 6, I found six eggs. These were all creamy white in color and were laid contiguous to one another in a horizontal position in the cell. By the middle of July, a few more larvae spun cocoons and on July 28, four more workers emerged. The appearance of these new workers presented an opportunity of allowing the bees the liberty of foraging for themselves, and so on July 30 the colony was released. The workers immediately assumed the duty of providing food for the colony, but the death on August 4 of the crippled old queen brought to a close its further development.

3. Experiment 13, 1919.

Only that part of this experiment relating to *B. impatiens* will be presented here, since this experiment will be more fully reviewed in another paper under the topic of queen substitution and mixed colonies. This experiment was begun originally with a queen of this species taken at Dongola, Illinois, on May 5. Prior to the time of her introduction into an artificial nest on May 25, the queen was kept in the customary manner to make her become

"broody." On May 27, the queen showed a great interest in the nest, and two egg cells were constructed on the pollen lump. The succeeding day, the cells contained eggs and were completely capped over in the usual manner. Larvae were first noticed in these cells on June 2, but it is probable that the eggs hatched before this date. An additional egg cell was prepared on this latter date and the colony seemed destined to a normal development. For several days afterwards, due to my unavoidable absence, this nest was not examined and when the nest box was next opened on June 7, I found the queen entangled in the cloth top of the artificial nest and almost dead. On being fed she revived, but displayed no further interest in the nest. In hope of arousing her interest in the comb by means of the presence of another queen, a queen of *B. bimaculatus* (Cresson) was placed in the nest on June 8. At first this ruse seemed to be successful, but on June 9 all trace of interest in the nest had again disappeared. Realizing the folly of further efforts to get the mother queen to nourish her young, I decided to use this comb for experiments in queen substitution. Accordingly, a queen of *B. auricomus* (Robertson) was added to the assemblage. Eventually the *bimaculatus* and *auricomus* queens became interested in the nest, but further information concerning this colony is out of place here. It should be added, however, that very small workers of *B. impatiens* emerged on June 26 and 28, under the care of the *B. auricomus* queen and continued on the best of terms with their foster mother. Both workers were very small and the one that emerged on June 28 was crippled, clearly showing the effects of malnutrition and the lack of attention during their infancy—the period from June 2 to June 10. One of these workers even lived to maintain friendly relations with workers produced by the *auricomus* queen.

4. Experiment 13, 1920

This experiment was begun on May 30 with a queen of *B. impatiens* received on May 10 from Dr. Hugh Glasgow of Geneva, New York. Previous to May 30, the queen had been prepared in the usual manner for colony production. Interest was immediately taken in the nest and on June 2 an egg cell containing several eggs was found in the nest. This cell was first observed to contain larvae on June 7. The colony progressed nicely until June 22, when I had to abandon it for various reasons. This

experiment was of interest only in that it demonstrated that queens of bumblebees of this species can be transported from one section of the country to another and be made to produce colonies under artificial conditions.

5. *Experiment 16, 1920*

In this experiment I used a queen of *B. impatiens* received on May 21 from Mr. C. A. Frost, of Framingham, Massachusetts. After the usual procedure preparatory to nesting experiments, the queen was placed in an artificial nest on June 6. On June 7, the queen manifested an interest in the nest and on June 8 the nest contained an egg cell with three eggs. The next day another egg cell was made and eggs deposited in it, and also an additional egg cell and eggs on June 10. Larvae were first observed on June 13 and these continued to develop until the study of the nest was abandoned on June 22. This experiment confirmed the fact (See Experiment 13, 1920) that queens can be shipped to various localities without interfering with their nest building instincts.

C. Biological Summary

1. *Resumé of Literature*

In keeping with the general status of our knowledge concerning the bumblebees as a whole, very little has been published regarding the habits of this common and widely distributed species. Cresson (1863) was the first entomologist to record the finding of a nest of *B. impatiens*. He states that the nest contained thirty queens, thirty-eight workers and thirty-four males. Besides noting the small size of the workers as compared with that of the queens and the lack of variation in the coloration of the different castes, he gives no information concerning the comb or habits of the bees. A year later (1864), Mr. F. W. Putnam recorded finding a nest of *B. virginicus* [=*B. impatiens*] "under an old stump in an orchard," but gives us no further details. He mentions, also, the capture of three males of this species which were "flying under a large tree on which they frequently alighted." He says further, "So much did these bees resemble large flies in their actions, that at first I mistook them for those insects." I am quite sure this latter note relating to the habits of the males refers to *B. separatus*. In 1863, Cresson described *B. impatiens* from all three castes, but the male he then described as this species

possessed very large eyes and differed in other ways from the female. Three months after publishing the description of *B. impatiens,* Cresson (1863b) had the opportunity to study a nest of this species found near Kaign's Point, New Jersey, on October 7, 1863. This led to the discovery of the true male of *B. impatiens* and the assignment of the male "Described under *B. virginicus*" to a new species which he named *B. separatus.* The fact that the males of *B. separatus* were described in 1863 under the name *B. virginicus,* explains Putnam's determination of the males he caught flying about trees in 1864 as this species. Accordingly, the habits Putnam recorded for the males of *B. impatiens* relate to *B. separatus* and prove to be in keeping with the habits of the males of *B. separatus* as I have observed them.

The next published statements regarding the biology of *B. impatiens* are those of Riley (1880) who identified a bumblebee caught robbing the "honey bees of their scanty stores" as this species. Eleven years later Howard (1891) reports finding large numbers of these bees attracted to the blossoms of the horse-chestnut and described their peculiar actions as probably being due to the toxic effect of the nectar.

Franklin (1913) reports having taken several nests of this species. He says that "as far as I have been able to ascertain, they are invariably subterranean and the colonies often consist of a very large number of individuals. The largest *Bombus* colony which I have ever taken belonged to this species, and was taken at Amherst, Massachusetts, August 31, 1904." In this colony he found four queens, fifteen males and three hundred and thirty-six workers. One hundred and fifty-four, of the three hundred and thirty unbroken cells in the nest, "were queen cells and the majority of the young inside them were still in the larval state." According to Franklin the queen cells averaged about eighteen millimeters in length, and, though the remaining cells varied considerably in size, they were "on the average a little more than one-half as long as the queen cells." The nest itself was made of old grass, in an old mouse burrow two and one-half feet below the surface of the ground.

Jackson (1920), says that "In October the males are practically the only representatives of the Bremidae to be found" and that the workers fly very late in the fall.

As far as I am aware, the only other contributor to a knowledge of the biology and habits of this species is Plath (1922).

This author records taking sixteen "nests of this species during the summers of 1921 and 1922." All of these 16 nests were subterranean as well as several others which were not dug up. "They were from 1 to 3 ft. below the surface, and had tunnels varying from 18 inches to 5 ft. in length. A number of these nests were situated in decayed stumps." Plath states, also, that these colonies were very populous and records one colony as having thirty-one males and fifty workers, a second with about one hundred and twenty-five workers, and another with more than four hundred and fifty workers. The workers are stated to appear about the first week in June "and the majority of the young queens and males hatch in August and September." It is interesting to note that Plath was impressed by the bellicose disposition of this bumblebee for he remarks in a footnote that this is "an exceedingly pugnacious species." My experiences with this species agree with the statement of Plath. In spite of many precautions I was stung by the workers on several occasions. The same trait in behavior finds its expression in the manner in which the workers attack *Psithyrus* queens introduced into their nests. In one experiment of this nature made by Plath, seventeen workers surrounded and attacked the intruding queen; so many in fact, that at least one of them met death through the ill-directed sting of its fellow worker.

2. *Anthophilous Habits*

The reader is referred to the valuable paper of Lutz and Cockerell (1920) for a summary of most of the records relating to the flowers visited by this polytropic species of bee. A few of Robertson's records have been overlooked in this list and these, together with those which have accumulated since then, are as follows:

Robertson (1890–1899): *Cephalanthus occidentalis, Libelia syphilitica, Campanula americana, Petalostemon violaceus, Delphinium tricorne, Dicentra cucullaria, Claytonia virginica, Viola padata* var. *bicolor, Dentaria laciniata, Impatiens fulva, Impatiens pallida, Tradescantia virginica, Erythronium albidum, Verbena stricta, Dianthera americana, Lythrum alatum, Hypericum cistifolium, Clematis virginiana, Clematis pitcheri,* and *Staphylea trifolia.* Jackson (1922): *Pontederia*

cordata, Chrysopsis mariana, and *Xolisma ligustrina.* Rau (1920) : *Aster multiflora.*

In addition to the already exceedingly numerous lists of plants frequented for nectar or pollen I have found this species on *Monarda fistulosa, Melilotus alba, Trifolium pratense* and *Ligustrum vulgare.*

3. Duration of the Developmental Stadia

In order to secure data regarding the duration of the developmental stadia of *B. impatiens,* one colony (Experiment 6, 1919) of this species was closely studied from its inception to its end. During the interim from May 22 to September 16, fifty-four examinations were made of the contents of all cells and cocoons comprising the comb. Although these examinations did not give a complete record of the development of all the stages of each bee produced by the mother queen, they were sufficient to present a good approximation of the duration of the various developmental stadia for the workers (females) and males. Since no queens were produced in this colony, on information regarding their developmental stadia can be given. Because the tables giving this data are extensive, only by deductions from them are presented. For a complete understanding of the nature of the complete tables, and how the essential data were secured, the reader is referred to a recent paper (Frison, 1928).

It was found that the egg stage is the shortest and the larval stage the longest of the three development stadia of the workers and males. The workers required between four and five days in the egg stage, twelve to fourteen days in the larval stage, and six to eight days in the pupal stage. The males averaged between four and five days in the egg stage, fifteen days in the larval stage, and eight days in the pupal stage.

The total time required for the production of the adults varied. It was from twenty-two to twenty-seven days for the workers and twenty-seven to twenty-eight days for the males. During June some evidence was obtained which indicated a lengthening of the life cycle.

4. Seasonal Appearance of the Castes

There is a difference in the time of appearance of the three castes of bumblebees. This is because only the queens are able to

hibernate and their first progeny are ordinarily workers. When writing about the seasonal appearance of the castes I have adopted the practice of considering first the time of the appearance of the old queens in spring, second the workers and lastly the males. This is their ordinary sequence in a calendar year. However, since the queens found in spring were produced in the preceding summer or fall another arrangement might be used. The chief objections to beginning an account of the seasonal succession of the castes at the time the new queens emerge from cocoons are the difficulty of securing data concerning this period unless colonies are reared, and the fact that hibernation must take place before any progeny can be reared.

The queens of *B. impatiens* are usually the second species of bumblebee to appear in spring in the vicinity of Urbana, Illinois. The honor of being first is possessed by the queens of *B. bimaculatus* (Frison, 1928). The earliest records I have for the queens of *B. impatiens* in Champaign and Vermillion Counties during a period of seven years are as follows: May 2, 1914, University Woods, Urbana; April 23, 1915, University Woods, Urbana; May 5, 1916, University Woods, Urbana; May 14, 1917, University Woods, Urbana; April 18, 1918, Brownfield Woods, Urbana; April 13, 1919, Mahomet, Illinois; and May 8, 1920, Oakwood, Illinois. This list gives a very good idea of the time the queens are first encountered in spring in this locality. The time of appearance is each year directly correlated with the advance or retardation of spring. The lateness of their flight varies in direct proportion to the time of their first appearance, establishment of a nest, and weather conditions. In this vicinity the old queens of *impatiens* are rarely encountered in the field after the end of June.

The workers are seldom seen out of doors before six weeks after the appearance of the queens. In 1919, cocoons of workers were found in a nest at White Heath, Illinois, on May 17. This place was but a few miles from the place where I first captured the first queen of *B. impatiens* of the season on April 13. Workers were caught in the Brownfield Woods in 1915, on June 6. This latter capture was just about seven weeks after the first queen of the season was collected two miles away. Workers continue to be encountered in the field as late as October; their lateness depending on the character of the fall weather. The earliest record I have for the appearance of the males in this vicinity is July 26, 1913, in the University Woods. Ordinarily the males

appear much later, and I have taken them at Champaign, Illinois, in 1911, as late as October 9.

The new queens usually appear at about the same time as the males but are seldom captured by collectors. This is because they speedily seek hibernating quarters and spend little time on flowers. Franklin records finding four queens—three or all of which must have been young queens—in a nest he opened on August 31, 1904, at Amherst, Massachusetts. Franklin states also that the nest contained "one hundred and fifty-four" queen cells and "the majority of the young inside them were still in the larval state." Cresson found thirty queens in the nest found at Kaign's Point, New Jersey, on October 7, 1863. These dates show that the queens are ordinarily produced in the late summer and early fall.

In most other parts of the range of this species in North America the same general sequence in the appearance of the castes takes place. I have records of the queens taken in North Carolina the 31st of March and in Georgia on March 21. These records show the influence of the warmer temperatures prevailing in the southern part of the range of this species. The same factors that cause an earlier appearance of the queens in the southern part of their range hasten the appearance time of the workers, new queen and males. Plath says that in Massachusetts the "majority of the young queens and males hatch in August and September." This statement is in agreement with my conclusions regarding the usual time of appearance of these castes. I have seen a male of *B. impatiens* from Miami, Florida, which was collected on February 6, 1903. Either this specimen has been erroneously labeled as to date or in Florida a modification of the general life history of this species occurs which is suggestive of bumblebee life in Corsica as it is pictured by Ferton (1901), in Sardinia by Krausse (1910) and in the state of São Paulo, Brazil, by von Ihring (1903).

5. *Caste Ratio*

The worker caste numerically dominates in this species. The largest number of workers I ever found at one time in Experiment 6, 1919, was on August 11 when there were one hundred and sixteen of them in the nest. According to my records, approximately two hundred and thirty workers were produced in this nest. The difference in number between the two figures just

cited is easily accounted for by the fact that many of the workers were out of the nest gathering nectar and pollen when the nest was examined on August 11. Some died from time to time, and on several occasions it was necessary to kill others. Approximately eighty males were produced in this nest; making a ratio of about one male to three workers. The development of queens would undoubtedly have changed this ratio.

In the nest examined by Franklin (1913) on August 31, 1904, at Amherst, Masachusetts, the number of workers, males and queens was, respectively: three hundred and twenty-one, fifteen, and four. Franklin says there were also one hundred and fifty-four queen cells and one hundred and seventy-six other cells probably destined to produced mainly males. Counting the cells as well as the adults the number was about approximately three hundred and twenty-one workers, one hundred and ninety-one males, and one hundred and fifty-eight queens. As the males and queens were apparently just emerging, their number is nearly correct. In the case of the workers I have no doubt that as many as four hundred were produced. If we accept this latter estimate for the number of workers, about two workers were produced to every male and eight workers to every queen. In the nest found by Cresson (1863) on October 7, 1863, at Kaign's Point, New Jersey, there were thirty-eight workers, thirty-four males, and thirty queens. The small number of workers in this nest was no doubt due to the lateness of the season.

In one of the nests found by Plath (1922) there were about four hundred and fifty workers, but no mention is made of the number of queens or males. In another nest this same author found seventeen males, about seventy-five workers, and several inquiline bees (*Psithyrus*). A third nest yielded thirty-one males, about fifty workers and many other insects. In these nests, it is apparent that the workers dominated.

6. Size of Colonies

The colonies of this species attain considerable size, as evidenced by the preceding records of Franklin (1913) and Plath (1922) and those of my own. Experiment 6, 1919, produced with certainty two hundred and eighty-three bees, and adults emerging from groups of uncounted cells must have numbered fifty more; making a grand total of over three hundred and twenty-five bees. In the nest Franklin studied there were three

hundred and forty bees, besides three hundred and thirty cells or cocoons containing various immature stages. The production of adults by the end of September in this latter colony would have been nearly seven hundred; truly a large colony of bees. Plath (1922) mentions one colony which consisted of four hundred and fifty workers on August 4, 1921. When small colonies of this species are found it is an indication of the influence of deleterious conditions, rather than a low rate of fecundity on the part of the queens of this species.

7. *Variation.*

B. impatiens is apparently not susceptible to marked color variations. In contrast to certain other bumblebees, too, the males and females are quite similarly colored. This is in keeping with their general color constancy or fidelity to design. The only color variation worth mentioning occurred in the case of three workers; one observed in a nest on July 7, and two others on August 22. These workers had the dorsum of the thorax covered with a bright orange-yellow pubescence instead of the usual pale, whitish-yellow color.

In respect to variation in size, however, this species is most interesting. As is customary with most species of bumblebees, the greatest range in size is exhibited by the worker caste. The variation in length of the workers may range anywhere from eight to seventeen millimeters. The most significant feature of this aspect of variation in this species is the fact that one never has difficulty in separating queens from workers as is sometimes the case with certain species. This may not always hold true, but such has always been the case with the many specimens I have collected, reared and studied in collections throughout the country. Franklin (1913) gives the length of the queens as sixteen to twenty millimeters, but most of the queens I have studied measured between twenty and twenty-five millimeters. The significance of this isolation in size between the queens and workers was discussed by the author in another paper (1927b). Briefly, in that paper *B. impatiens* was considered as a species with a high fecundity in the queen caste and with a rudimentary specialization of the more highly developed caste system of the honeybee. As a general rule, the males are as large as, or slightly larger than, the workers, but much smaller than the queens. A variation, however, may occur in the size of the males even from the same nest; an indication that trophogeny plays an important

role in the size of the adults. For instance, two of the males found in Experiment 6, 1919, on September 5, were only nine millimeters in length; whereas certain other males were fifteen millimeters.

In order to get data relative to the extent of variation in the male genitalia (structural characters of much importance in systematic investigations) of individuals from the same nest, ten males showing considerable variation in size were selected from forty-seven removed from Experiment 6, 1919, on September 5. The genitalia of these males varied in size in proportion to the size of the bee, but no noticeable variation in their form was discernible. Other characters such as those offered by the malar space and antennal segments indicated the same structural constancy. Freak individuals may appear, but their crippled condition is due to malnutrition, injury to pupae, etc.

8. Cocoons and Food Storage

Silken cocoons are spun by the larvae about two days before pupation. Although some silk is spun by larvae previous to the spinning of the cocoons, it is only for the purpose of holding together the elastic wax-pollen walls of their cells. Since many eggs are laid in a single cell it is evident that at least for a short time after the larvae hatch that they occupy the same wax-pollen cell. After a short time the larvae begin to separate from one another and strands of silk become evident in the wax-pollen cells which surround them. As the larvae increase in size the silken threads become more numerous, and when larval growth is completed the cocoon is rapidly spun. These cocoons, dirty yellow in color, are the most conspicuous part of a bumblebee nest. They vary in size just as the adults do, some being large and others small. Three worker cocoons measured on July 23 were twelve to fifteen millimeters in height and eight to nine millimeters in breadth.[1] As is the case with the other species which I have studied, the wax-pollen necessarily coating the cocoon when first spun is soon removed by the bees and used elsewhere. When a worker is ready to emerge it partly cuts off with its mandibles the upper part of the cocoon. I have never seen workers on the comb assisting in this operation. After the bee has emerged the cocoons are completely renovated and both honey and pollen

[1] Two male cocoons measured on September 16 were, respectively, ten to twelve millimeters in height and four and one-half to five and one-half millimeters in breadth.

are stored in them. Cocoons so stocked with provisions are then often closed over on top by the wax-pollen used so generally in the comb construction.

With the gradual increase in size of the comb and the development of workers, the original honey pot made by the queen becomes insufficient to meet the needs of the colony and others are constructed. In Experiment 6, 1919, the first of these additional honey pots (Figure 6) was built alongside of the artificial one, but later in the season others were erected around the edge of the comb. During the early part of the season most of the surplus honey was stored in the honey pots, but later cocoons were also utilized for this purpose. Most of the surplus pollen was stored in empty cocoons near the center of the nest, but some was also stored in wax-pollen cells. The habit of storing the pollen in cells or cocoons apart from the clusters of larvae, caused Sladen to call the English species having this habit " Pollen-storers." Plath (1927) has coined the term " Amarsipoea " as a substitute for " Pollen-storers." As recently pointed out (Frison, 1928) the sectional name *Anodontobombus* Krüger (1917 and 1920) can probably be used for biological and morphological classifications.

9. Mating.

I have never witnessed the mating of males and females of this species, but a male and a queen of this species captured *in coitu* are in the insect collection of Purdue University at Lafayette, Indiana. These bees were taken at Lafayette on September 25, 1915. The late production of the queens and males of *impatiens* makes late matings unavoidable; a seasonal adjustment quite different from *bimaculatus* whose males and females are produced and mate in mid-summer (Frison, 1928).

10. Nesting situations.

There is very good evidence to indicate that the queens of this species prefer to nest beneath the surface of the ground. All of the nests taken by Franklin (1913) and Plath (1922) were subterranean. Plath says that the nests he studied were reached by " tunnels varying from 18 inches to 5 ft. in length." The nest found by Putnam (1864) was located under an old stump. The colonies I had under observation were started in artificial nests and others occupied artificial domiciles buried in the ground (Frison, 1926). No doubt other nesting sites than those under the ground are occasionally used by the queens in the cases of necessity.

11. Hibernation.

Thus far the writer has never been fortunate enough to find hibernating queens of this species of bumblebee. Plath (1927), however, has published some exceedingly important observations regarding this phase of their biology and reports that under normal conditions the young queens of this species hibernate in the soil near the entrance to the maternal nest. He further states that from thirteen to forty queens hibernated in a small space near the entrance of a former nest. These observations confirm a story told me by a young eastern entomologist, whose name I have forgotten, that he once found nearly a hundred queens of *B. impatiens* hibernating in a small area in sandy soil near New York City.

12. Domestication.

This species is well adapted for domestication, or semi-domestication. Experiments reported in this paper and elsewhere (Frison, 1927a) demonstrate that queens of *B. impatiens* can be induced to start colonies in artificial nests without the aid of workers and that the queens can be attracted to artificial domiciles (Frison, 1926). Additional evidence of the suitability of this species for domestication has been published by Plath (1923).

In contrast to *B. bimaculatus* which is also easily reared under controlled conditions (Frison, 1928), *B. impatiens* is a most promising species from the standpoint of the possible economic exploitation of bumblebees. The colonies of this species are started early in the season and continue until fall, the species has a wide natural distribution, the colonies are large, and the bees are well suited for the pollination of such valuable crops as red clover. The species likewise offers exceptional advantages to the laboratory worker.

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Plates XXIV–XXVI.

Figure 1. Start of the comb of *Bremus impatiens* under controlled conditions, showing: *a,* the pollen lump containing the first egg cells and eggs; *b,* the artificial honey pot. May 2 (From Biol. Bull., 1927, p. 55).

Figure 2. Comb of *Bremus impatiens* of about two weeks' development, showing: *a,* several eggs in the same cell; *b,* one of the first larval cells; *c,* groove caused by the queen brooding on the first larval cells. May 10 (From Biol. Bull., 1927, p. 57).

Figure 3. Comb of *Bremus impatiens* of about six weeks' development, showing: *a,* wax-pollen pots for the storage of honey; *b,* empty cocoons used for the storage of honey and pollen; *c,* groups of various-sized larvae. June 10.

Figure 4. Comb of *Bremus impatiens* after the climax development has passed, showing: *a,* empty cocoons; *b,* larval cells; *c,* wax-pollen pots; *d,* wax-pollen shield. September 6.

Figure 5. Comb of *Bremus impatiens* in large observation box. September 6.

Figure 6. Wax-pollen honey pots of *Bremus impatiens.* One of these was the first honey pot constructed by the queen. Enlarged 5 ×.

Figure 7. Queen of *Bremus impatiens* " carding " materials over comb.

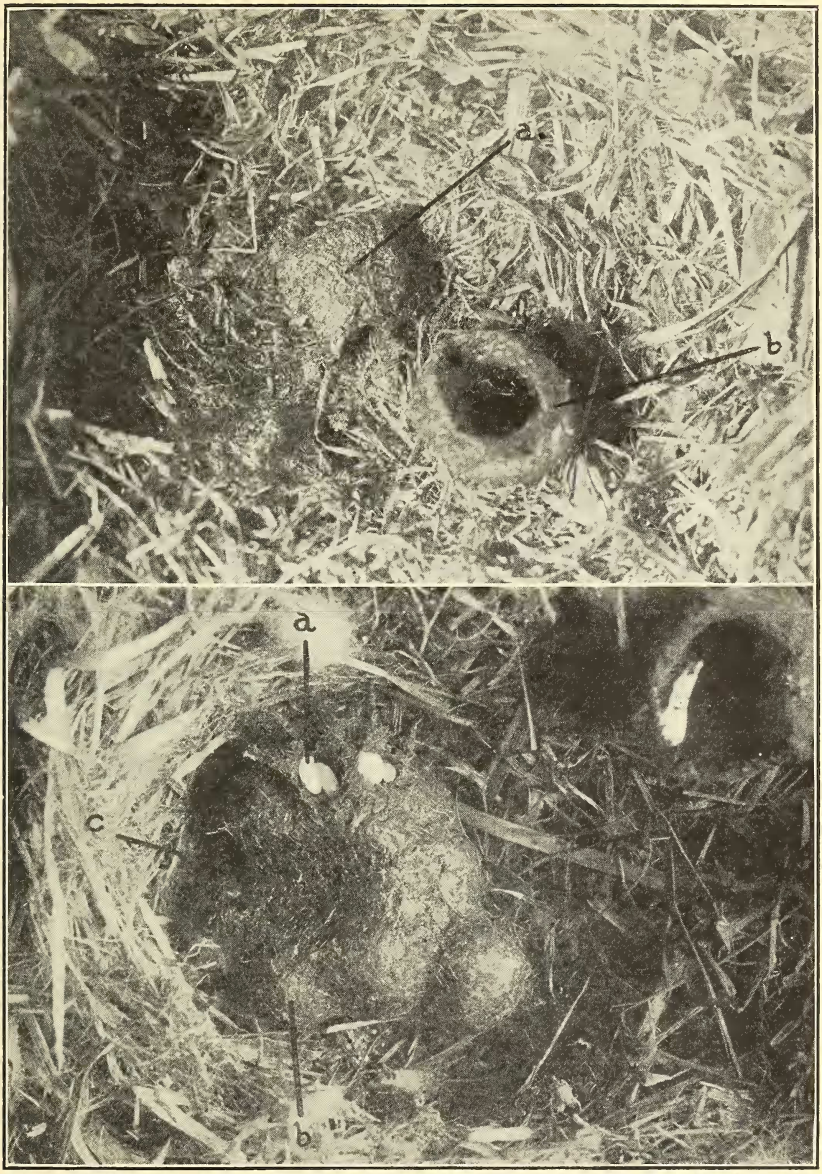

Fig. 1—Upper = Fig. 2—Lower

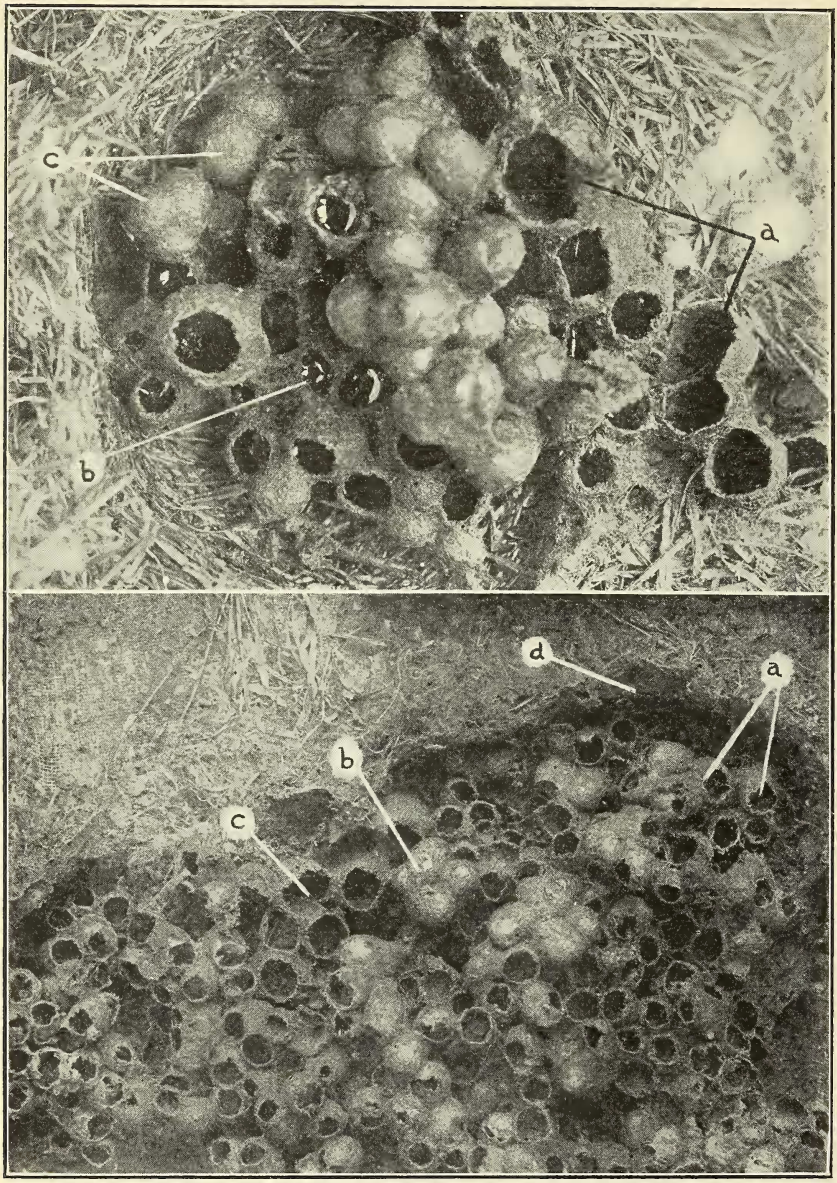

Fig. 3—Upper = Fig. 4—Lower

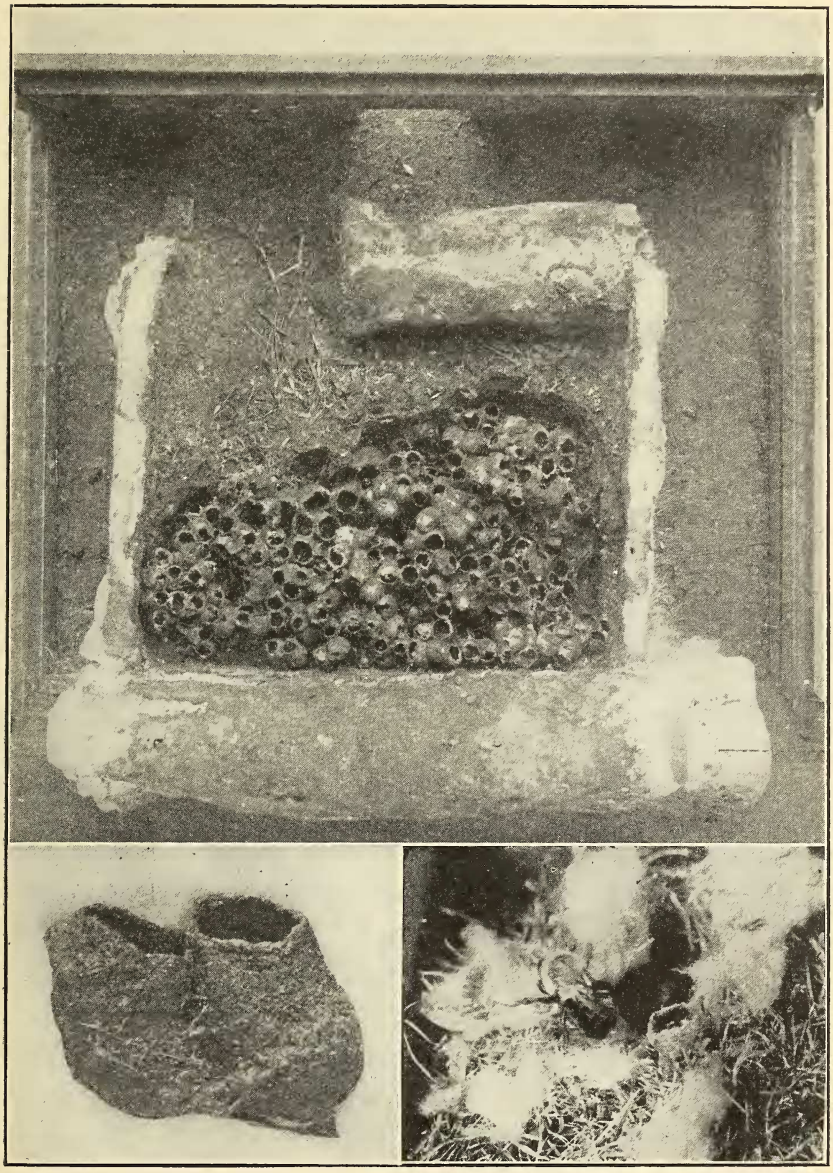

Fig. 5—Upper. Fig. 6—Lower, left. Fig. 7—Lower, right